Growth Types and Growth Activities of Shoots, Needles and Cambium in the Genus *Pinus*

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マツ属における伸長型と主軸伸長，針葉伸長，肥大生長の季節変化

大　畠　誠　一

Résumé

In relation to distribution and speciation in the genus *Pinus*, seasonal growth of shoots, needles and cambium of 28 pine species was measured, which had been planted under natural condition at Kyoto. The growth course of their organs were fundamentally divided into two patterns by the shoot growth type, uninodal and Taeda type. Pines of uninodal type showed one single flush of growth in shoot and needle in the same growing season, whether early or late in seasonal variations. In pines of Taeda type, new shoots and new needles flushed repeatedly in the same season. The two growth patterns seemed to be sustained respectively by the two different cycles of carbohydrates budget through the year. In the uninodal pines, the growth cycle seemed to be sustained mainly by stored food, which pines might be more adapted to northern region. The growth cycle of Taeda type may be advantageous to warmer climate region.

要　　旨

マツ属の分布と種分化に関連して，28種のマツの主軸伸長，針葉伸長，幹の肥大生長の各生長間の相互関係を検討した。

マツ類の生長タイプを大まかに分けると，単節型とテーダタイプに分けられる。単節型のマツ類は，1生育期に1回の主軸伸長と針葉伸長を基本とする。一方，テーダタイプは，1生育期に多数回の主軸伸長とそれに対応した多数回の針葉伸長を示す。両タイプは，異なる気候条件に適応したふたつの典型的生長タイプとみなされた。年間を通じての生産物配分からみると，単節型のマツ類は，夏以後に主軸伸長，針葉伸長を停止する種類が多く，それ以後に生産した物質を翌年にもちこす機構を有し，生育期間の短かい気候に適応した生長様式をもつとみなされた。一方，テーダタイプの典型は，極論すると物質蓄積の機構をもたず，適時生長するという，生育期間の長い，暖かい気候に適応した生長様式を有すると解釈された。

Introduction

The genus *Pinus* is one of the most widely distributed genera of trees in the Northern Hemisphere between the polar region and tropics. It consists of more than hundred species and is the genus with the greatest number of species in the family of *Pinaceae*. Such a differentiation may be the result of a speciation and adaptation to the environmental conditions of a broad climatical range.

The aspect of taxonomic signification of the high differentiation of pines has already been discussed by SHAW[1)] and MIROV[2)], and distributional maps have been compiled by CRITCHFIELD and LITTLE[3)]. In relation to the evolutional aspect of the genus *Pinus*, further informations seems to be needed.

Adaptation of each species may be expected in the seasonality of growth of the individual organs, as well as in the morphological differentiation of organs. Furthermore, there may some reciprocal relations in the growth of individual organs. The present study examines elongation growth of the leader and needles, and cambium growth of 28 species of pines in order to distinguish growth type which can be related to the geographical distribution and underlaying adaptional trends.

The pine shoot growth is very complicated one in the pattern being different from the other genera of *Pinaceae*. Although 10 patterns of shoot growth have been proposed by LANNER[4)] containing two seedling patterns, it is difficult to make the clear distinction in them among many pine species. There may be a medical patterns in them, when we divide in detail the shoot growth pattern. In a recent study, SWEET and BOLLMANN[5)] proposed the two usages of the term "free growth" for pines not to restrict by a limited complement of preformed primodia and the term "predetermined growth" for the pines of fixed by LANNER[4)].

Lanner's division of shoot growth pattern and usages of two terms may not be appropriate for the examination of growth seasonality. The former is too minute and latter is too simple. To compare the growth seasonality, the author, here, divided tentatively into three pine groups founding on the shoot growth habit and needle growth habit, i. e., uninodal, Taeda and Contorta types as shown in Table 1. Uninodal type is mainly characterized by a monocyclic shoot growth and monocyclic needle growth as represented by Resinosa pattern by LANNER[4)], though some scale leaves rarely grow at the base of the winter buds. Adding this pattern, uninodal type contains the pines of Pinaster pattern and Pinõn pattern by LANNER's grouping. The shoot growth of Pinaster pattern is initiated, however, in the winter, long after those of the first cycle (LANNER[4)]), the needle growth does not start untill the next spring. On the other hand, most species of Pinõn pattern are characterized by the rarely small addition of minor shoot to the spring shoot, but the flush of needle growth are rather monocyclic.

In some pines, the buds flush repeatedly in the same season. As the result of this growth, new shoot makes many internodes (multimodal shoot growth by SHAW[1)]). In the pines of this type named by the author as Taeda type (OOHATA[6)]), the needle flush

Table 1. Pine species* examined the leader, cambium and needle growth, mean length of needles measured and shoot growth types.

	Tree age	Tree height (m)	Mean lengh of needles (cm)	Shoot growth type
SUBGENUS *STROBUS* Lemm.				
SECTION *STROBUS*				
SUBSECTION *CEMBRAE* Loud.				
Pinus koraiensis Sieb. & Zucc.	22	3.0	10.2	Uninodal type
SUBSECTION *STROBI* Loud.				
P. strobus L.	9	1.7	8.6	U
P. monticola Dougl.	5	0.8	9.3	U
P. armandii Franc.	5	1.2	12.3	U
P. griffithii McClel.	5	0.8	10.7	U
P. morrisonicola Hayata	6	1.2	6.9	U
SECTION *PARRYA* Mayr				
SUBSECTION *GERARDIANAE* Loud.				
P. bungeana Zucc.	22	1.6	6.0	U
SUBGENUS *PINUS*				
SECTION *TERNATAE* Loud.				
SUBSECTION *PINEAE* Shaw				
P. Pinea L.	4	0.5	8.2	U
SUBSECTION *CANRIENSES* Loud.				
P. roxburghii Sarg.	10	1.1	23.9	U
SECTION *PINUS*				
SUSECTION *SYLVESTRES* Loud.				
P. nigra Arnold	9	1.8	12.6	U
P. mugo Turra	16	0.6	4.2	U
P. pinaster Ait.	4	1.7	22.9	U
P. densiflora Sieb. & Zucc.	6	1.3	8.4	U
P. thunbergiana Franco	6	1.5	12.1	U
P. massoniana Lamb.	5	1.5	13.9	U
SUBSECTION *AUSTRALES* Loud.				
P. taeda L.	9	2.4	17.7	Taeda type
P. echinata Mill.	4	1.2	9.4	T
P. rigida Mill.	9	2.0	10.2	Contorta type
P. elliottii Engelm.	9	2.3	20.2	T
SUBSECTION *PONDEROSAE* Loud.				
P. ponderosa Laws.	22	2.4	13.1	U
P. hartwegii Lindl.	4	1.0	11.2	U
P. engelmannii Carr.	4	0.8	28.5	U
SUBSECTION *CONTORTAE* Little & Critch.				
P. banksiana Lamb.	9	1.9	3.1	C
P. contorta Dougl.	5	1.1	4.7	C
P. virginiana Mill.	4	1.1	5.0	C
SUBSECTION OOCARPAE Little & Critch.				
P. radiata D. Don	7	1.8	12.3	T
P. patula Schiede & Deppe	4	1.0	13.5	T
P. greggii Engelm.	4	1.6	11.4	T

* Classification of pines according to CRITCHFIELD & LITTLE (1966).

in the same season from their new shoots. This type contains three patterns of shoot growth i. e., Caribaea pattern, Elliottii pattern and Echinata pattern by LANNER[4].

The second group of fixed growth was named Contorta type after LANNER's Contorta pattern. The growth course of this type is same to uninodal type, but the annual shoot of this group is clearly multinodal (many internode) as shown by VAN DEN BERG and LANNER[7]. In these species, no needles start to grow untill next spring.

Materials and methods

For the measurement of shoot, needle and cambium growth, the pine species indicated in Table 1 are selected out of 80 pine species from all the world which are planted at Kamigamo Experimental Station of Kyoto University (latitude 35° 04′, altitude 180m). The mean annual temperature of the Station is 15.5℃, and annual precipitation is 1720mm.

During the growing season from end of March to October 1973, the growth of top leader elongation was measured at intervals of about 10 days, the growth of needles and cambium of same pines was measured during the following growing season, together with additional measurements of leader growth.

The elongation of the leader was determined by measuring the distance from the top of the growing shoot to a reference point at the older part of the main axis marked by a

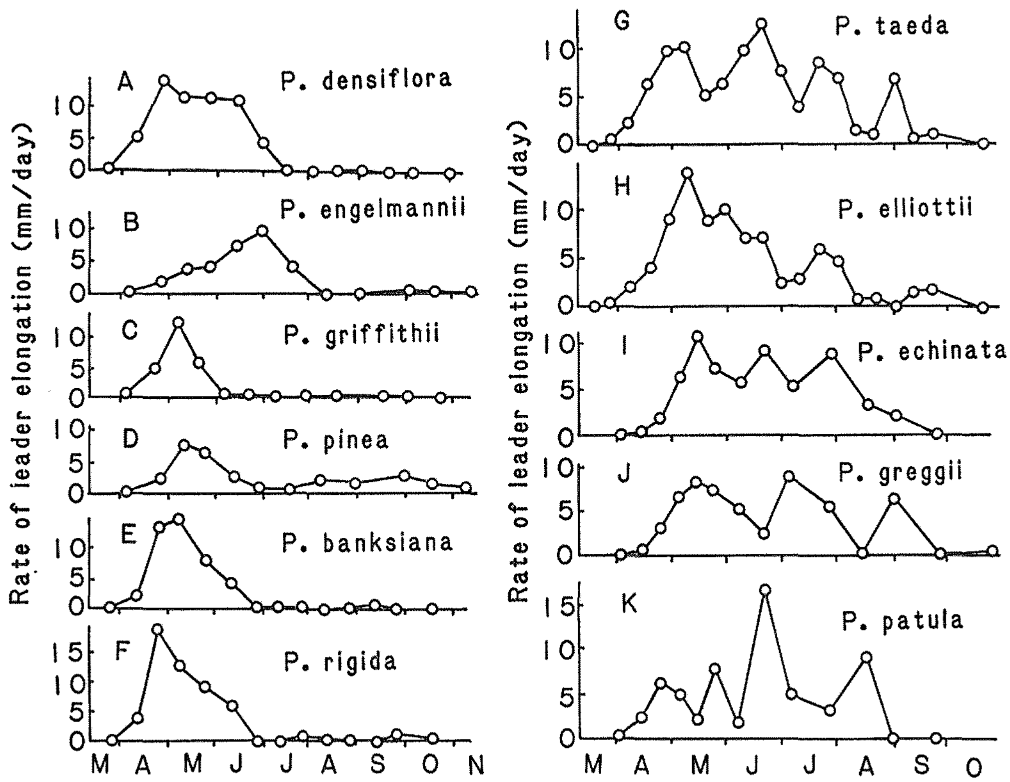

Fig. 1. Seasonal courses of leader elongation of uninodal (A-D), Contorta (E,F) and Taeda type pines (G-K).

stainless insect pin. The needle elongation was measured by comparing the average length of samples collected from the middle part of new shoot at regular intervals. The samples of multinodal pines were selected from the first (lower) internode, in order to compare to those of uninodal pines. The activity of cambium was determined by diameter measurements using a slide calliper at marked point in the middle part of two-year-old stems.

Results

(A) Leader and needle elongation

The buds of the different pine species at Kyoto started to swell nearly at the same time (end of March, see Fig. 3) , when the daily temperature was about 10 ℃. The shoot growth of the most species reached once their highest rates at early May and slowed down from end of May to June. In uninodal species, after termination of leader elongation, the terminal but for the next flush was formed from summer to autumn (Fig. 1, A -D) . Although most of uninodal pines showed this pattern of shoot growth, there were slight differences among species: in *Pinus engelmannii,* originating from Mexico, the leader elongation ceased later than in the other uninodal pines (Fig. 1, B) . In *Pinus pinea,* the slight elongation in late summer and autumn is due to the formation of a very long winter bud, which is characteristic for this species (Fig. 1, D) and *Pinus pinaster* (LANNER) [4]. It is characteristic for uninodal pines that the newly formed buds and leaf primodia never start to flush the same growing season. Therefore only one single internode is developed in one growing season. The 18 of 28 pines belong to this type (see Table 1) .

In pines of Taeda type, new buds flush repeatedly in the same season as reported by SHAW[1]. One typical pattern of Taeda type (TANAKA[8] et al.) is shown in Fig. 1, G-K. In this type, number of flushes is not always the same even in the same species (cf. LANNER[4]) and as shown in three samples of *Pinus elliottii* and *Pinus greggii* (Fig. 2). The extension of the first (lower) internode in some species was usually larger than that of the latter sprouting (upper) internodes. Among the Taeda type, this pattern is characteristic for pines originating from cooler regions. In other species, the mid summer growth was always as large as the spring growth or even larger. Because there are progressive variations by the species adapting to the climatical environment, pines of this type were lumped together in one group in this paper. The pines of this type belong mainly to subsection *Australes* and subsection *Oocarpae* (Unpublished data, OOHATA). Some pines, such as *Pinus halepensis* and *Pinus insularis,* in subsection *Sylvestres* showed this growth type.

In the second type of fixed growth, as shown in Fig. 1, E and F, shoot elongation in *Pinus banksiana* and *Pinus rigida* was same as in uninodal pines, but the annual shoot of these species was clearly multinodal (many internodes) . In these species, the multiple branch nodes formed in the winter bud. The "Contorta type" according to observation of SHAW[1] occurs in the subsection *Contortae* and *Sabinianae.* Unfortunately, of the subsection *Sabinianae* no species were available at the Kamigamo Station. *Pinus virginiana* of the substction *Contortae* showed a intermediate pattern between the Taeda and the Contorta

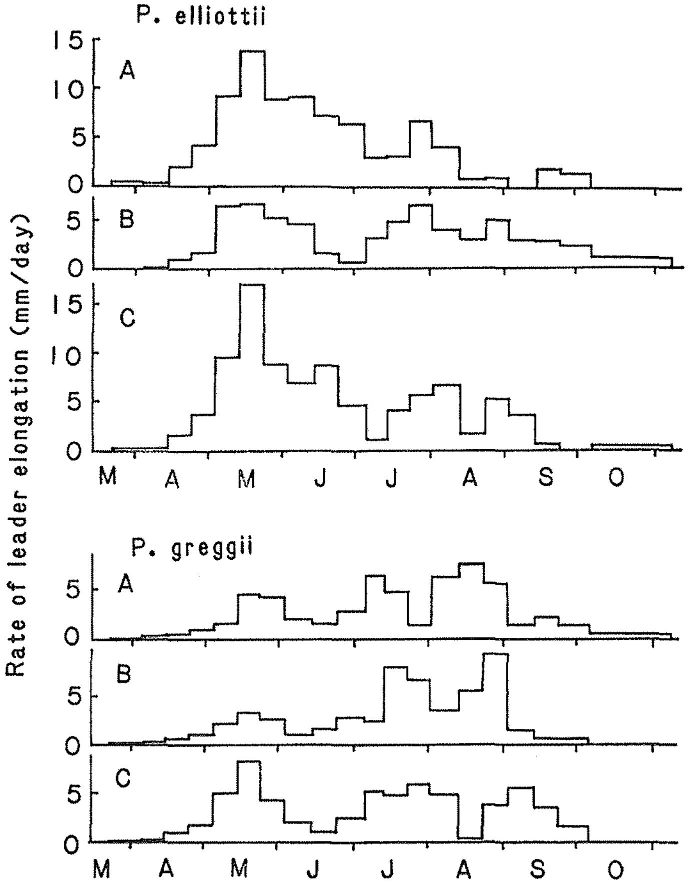

Fig. 2. Three spmples of seasonal course of leader elongation in respective two species of Taeda type. The rhythums of shoot growth were different between the two species and were slightly different even among individuals in the same species.

type (Fig. 5, F) .

Growth period of shoot affected by the shoot growth type, as shown in Fig. 3. Growth period of Taeda type species had, generally, long period, as the results of flushing the new buds. According to KOZLOWSKI[9], some southern pines in United States (pines of the Taeda type) made measurable hight growth over a 5 month period.

Needle elongation in most pine species began simultaneously immediately before the termination of the shoot growth at the end of June. The needle growth of the Taeda type species has only been measured with samples collected from the first internode. No peculiar feature among pines or types of shoot elongation has been noticed, except of different growth rate and growing period. Pine needles elongated, more or less, by stable rate. *Pinus banksiana* was the species with the lowest growth rate (0.7mm/day, Fig. 6, C) , *Pinus engelmannii* the species with the highest rate (3.5mm/day, Fig. 4, K) .

Needle elongation is checked by poor sources of carbohydrate in the first few weeks

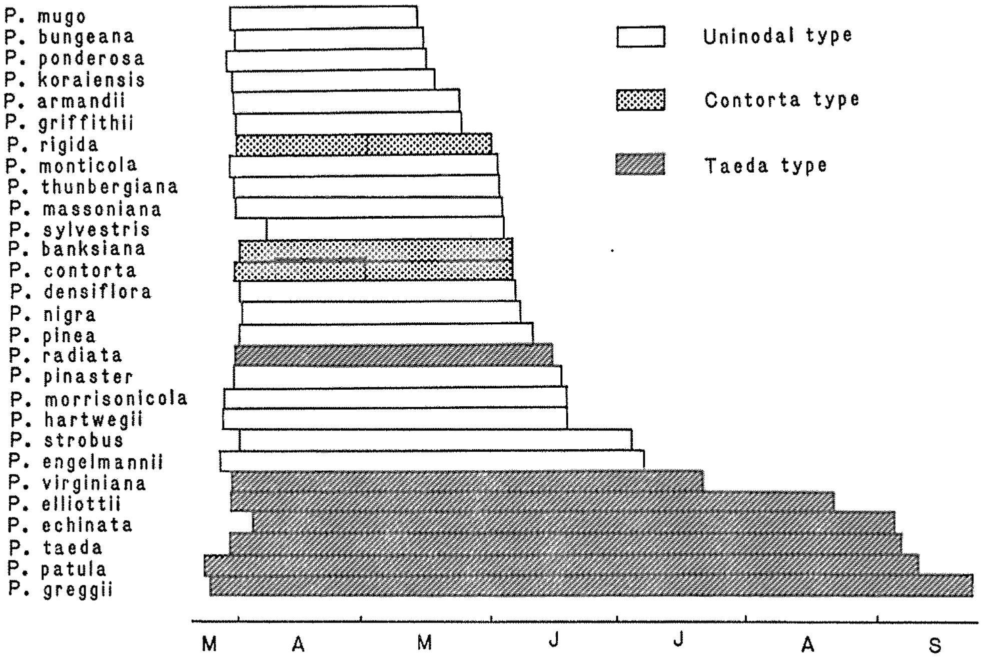

Fig. 3. Shoot growth periods and shoot growth types in 28 pine species.

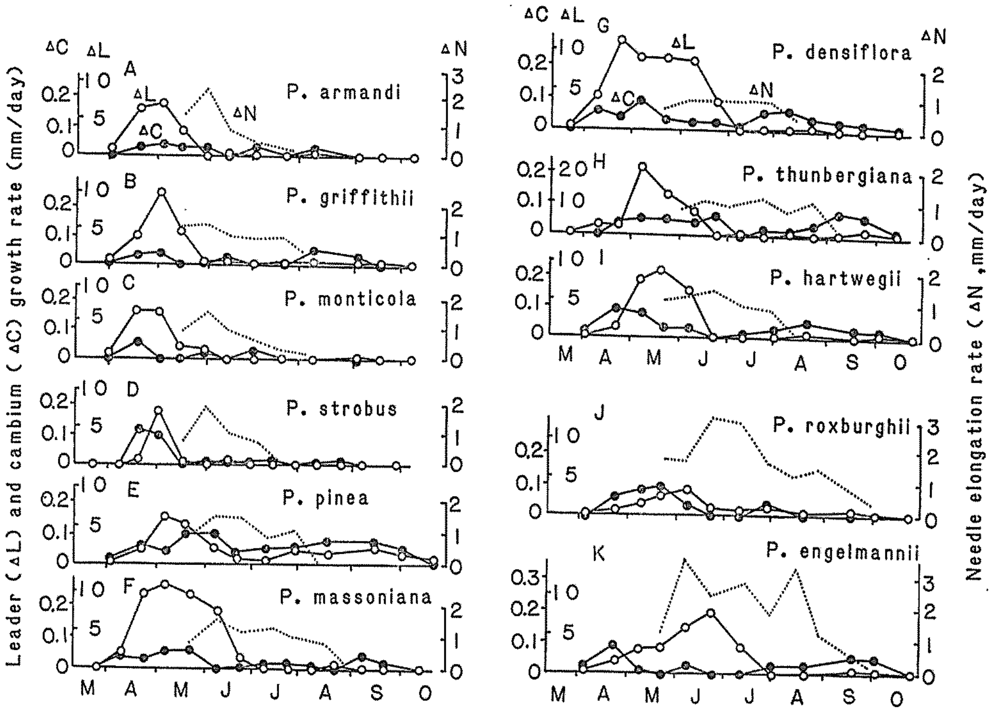

Fig. 4. Eleven samples of seasonal growth course of leader, needle and cambium in uninodal pine species.

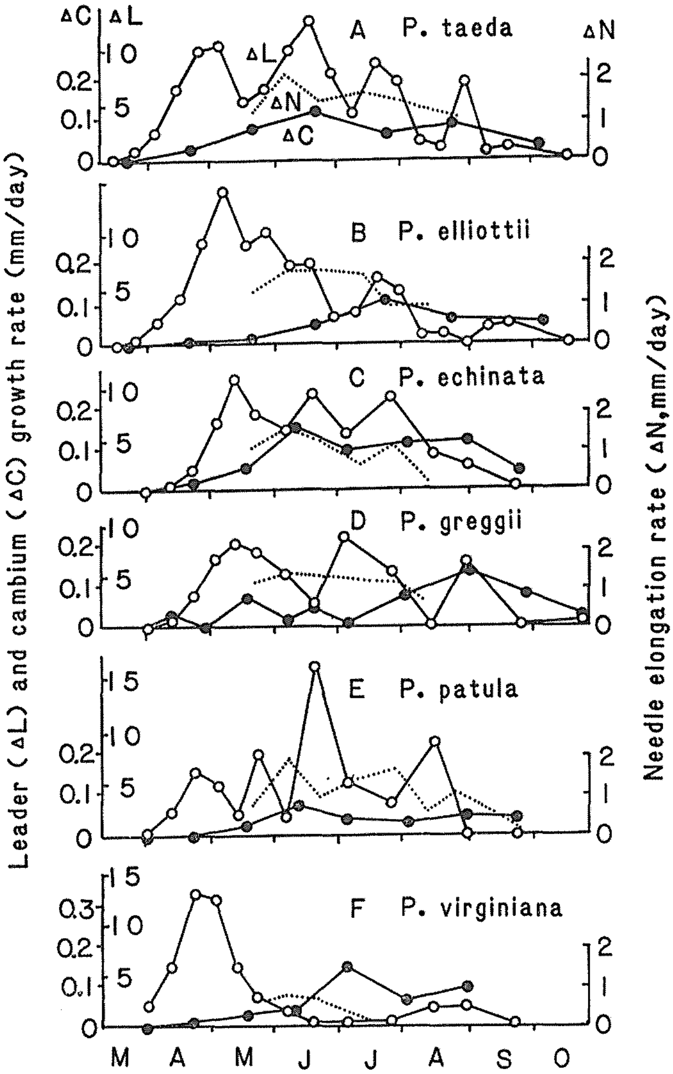

Fig. 5. Interrelations among leader elongation, cambium growth and needle elongation in pines of Taeda type (A–E) and intermediate type (F) between Taeda and Contorta type.

(GORDON & LARSON[10], ONAKA[11], FURUNO[12,13]), low temperature in autumn and water stress (GARRETT & ZAHNER[14]) . Although the completion of the growth of individuals in *Pinus contorta* was somewhat different by the provenances (CANNELL[15] et al.), the difference among species was larger than intra specific variation. There was a striking interrelation between high growth rate and long growing period of needles. Pines of warmer origin have a tendency to have longer needles (OOHATA[16], Table 1) . The needle length of pine correspondes to the length of the growing season at the place of origin. Very long needles are the results of high growth rate and long growth period. Therefore pines originating from regions where climatic stress (e. g. low temperature, drought)

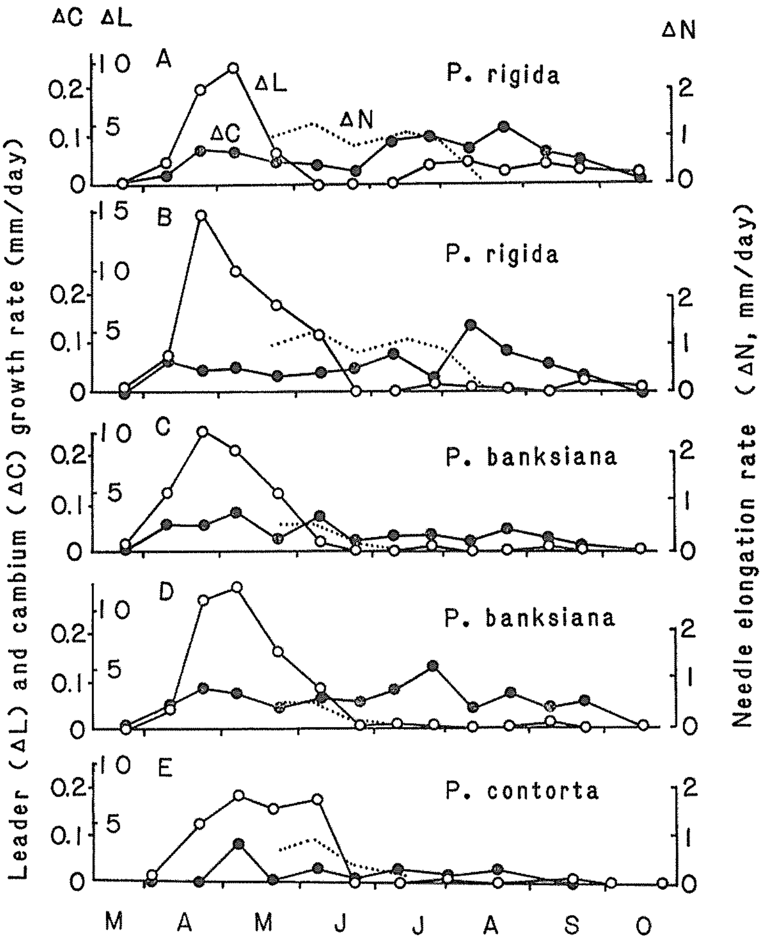

Fig. 6. Five samples of seasonal growth course of leader, needles and cambium in three pine species in Contorta type.

reduce the favourable period of the year, have shorter needles. The needle length of each species measured at Kyoto was about the same as measured by SHAW[1], who collected his material at the original place of the species. The high growth rate, long period of growth and long needles in southern pines may be a response to warmer climate.

Although as a rule needle elongation of northern pines ceases in summer, needles of Taeda type species continue growing till to the end of the growing season from new internodes. Therefore, the amount of new leaves in Taeda type species increased gradually toward the autumn.

(B) Cambium growth

In most of the investigated species, the cambium growth began at the end of March about the same time of the start of shoot elongation, and increased rapidly to a first maximum in May. The growth after the first maximum was different depending on the types of shoot elongation.

In species of uninodal type, the growth rate decreased in July or August, and increased to a second maximum in August or September. During October, the growth rate decreased gradually and ceased (Fig. 4) .

In the Taeda type, the cambium growth was low in spring, and it increased in summer or autumn as shown in Fig. 5. There was no clear decrease of the rate in summer in all species of this type.

The growth rate of cambium in pines of the Contorta type continued, more or less, in an equal rate from spring to autumn (Fig. 6, A-E) . These curves resemble rather of Taeda type than uninodal type.

Discussion

When leader elongation, needle elongation and cambium growth in the same pine species are compared, an interesting interrelation can be seen.

In every pine species, first to begin growth was the leader and about at the same time also the cambium, followed by the needles. Uninodal and Contorta type species started with fast growth at early April. As already noted by KIENHOLZ[17)] this high spring activity is probably due to the ready availability of a large amount of stored food. According to KOZLOWSKI[9)], shoot growth of conifers depends on food reserves in stem tissues and old needles, carbohydrates currently produced by old needles, or all of these sources. On this phase of nutrition, there are many previous studies by radioactive tracers SHIROYA[18)] et al., URSINO[19)] et al., GORDON & LARSON[10,20)].

Growth activity decreased to a low rate in summer. This appears to be associated with depletion of reserve materials, primarily of starch, in the trees as found in *Abies* trees (LOACH & LITTLE[21)]) . This depletion during early summer has been established in stems of *Pinus densiflora,* a species of the uninodal pine (SHIMAJI[22)]) and young *Abies* trees, a uninodal growth species (KIMURA[23)]) . From the previous results using isotope technique (NELSON[24)], URSINO & PAUL[25)]), translocation of assimilated matter to root in young pine (*Pinus strobus*) became low in late spring and early summer, when the new shoots grow. Although GLERUM & BALATINECZ[26)] reported that the photosynthete produced during the autumn contributed substantially more to respiration than to the bulildup of reserves, a fairly amount of assimilated ^{14}C was translocated to roots in long period of autumn (NELSON[24)]). A considerable amount of surplus matter may be accumulated for the reserves.

Needle elongation of most species of the uninodal type began when the growth rates of leader and cambium were decreasing (Fig. 4). LOACH and LITTLE[21)], KIENHOLZ[17)] and many results by radioactive tracer suggest that most of the material for needle growth at the beginning of needle development was synthesized by the old needles, and later by the newly developed needles. The second surge of the cambium growth starts in late summer, which seems to be sustained mainly by material supplied by the newly developed needles. As these needles become more active photosynthetically through the growth, a greater part of the surplus carbon budget can be stored for the next flush. The process of food store from summer to autumn in *Pinus densiflora* had been investigated by

SHIMAJI[22].

The above mentioned interrelation may be convenient for many uninodal pines distributed to temperate zone with clear limitation of the growing season. This behavior is, however, not suitable for pines distributed at lower and higher latitudes, even in uninodal species such as *Pinus engelmannii, Pinus roxburghii, Pinus strobus* and *Pinus monticola* (Fig. 4, C, D, J, K) . Compared with other uninodal pines, the leader elongation of these pines from lower latitudes was rather slow in spring. The maximum elongation rate of these pines was in June, i, e., about a month later than in the other uninodal pines. On the other hand, the needle growth of these species was continued till early October, i. e., about a month more than the other uninodal pines. The reason for the slow spring growth rate may be shortage of stored matter in the tree due to active needle growth in late autumn. This trend of growth seasonality seems to be one life pattern seen in uninodal pines to adapt to the low latitudes. In some pines from the cooler regions, the second surge of the cambium growth in autumn was indistinct (Fig. 4, C, D) The reason for the low rate for these pines may be shortage of phptosynthete by high respiration during summer in Kyoto.

In pines of the Taeda type, interrelation of growth activitiy from that of uninodal type, as shown in Fig. 5, the shoot elongation in spring was not always largest, and the cambium growth slow in the first surge. In summer or in autumn, the cambium activity become highest, when the amount of new needles was completed. Because the needle developed progressively on the new shoots sprouted from new buds, the needles growth was most active in summer and continued till late autumn. This behavior of leaves in Taeda type may be similar to that of cambium and leader growth. As in the southern species of the uninodal type, also in pines of Taeda type, the active growth in late autumn must have a delaying effect on the growth at the next spring. In other words, pines of this type do not have a priority mechanism for food accumulation.

Although the interrelation of growth activities in pines of the Contorta type was similar to those of the uninodal pines as shown in Fig. 6, the cambium growth continued actively till autumn as in the species of Taeda type.

As already examined by NAKAI[27] et al., volume growth completion of 2nd-year cones from warmer regions was later than those from cooler climates. Growth rates of cones in five sample pines are shown in Fig. 7 with the growth rates of leader, needle and cambium from the former results by NAKAI[27] et al. High growth rates in pine cones from cooler region such as *Pinus contorta* and *Pinus strobus* began after the high spring growth·of cambium and leader elongation. On the other hand, the maximum growth rate in *Pinus taeda,* a pine from warmer region, showed in summer when the needles elongated fairly long and the cambium growth was increased (Fig. 7, E) .

Cone growth from cooler region may be depended on food reserved former season and currently produced by old needles. On the other hand, main growth in *Pinus taeda* may suggest that the fairly part of the growth depends on carbohydrates currently produced by new needles.

The interrelation of the growth activities can be considered as a manifestiation of the

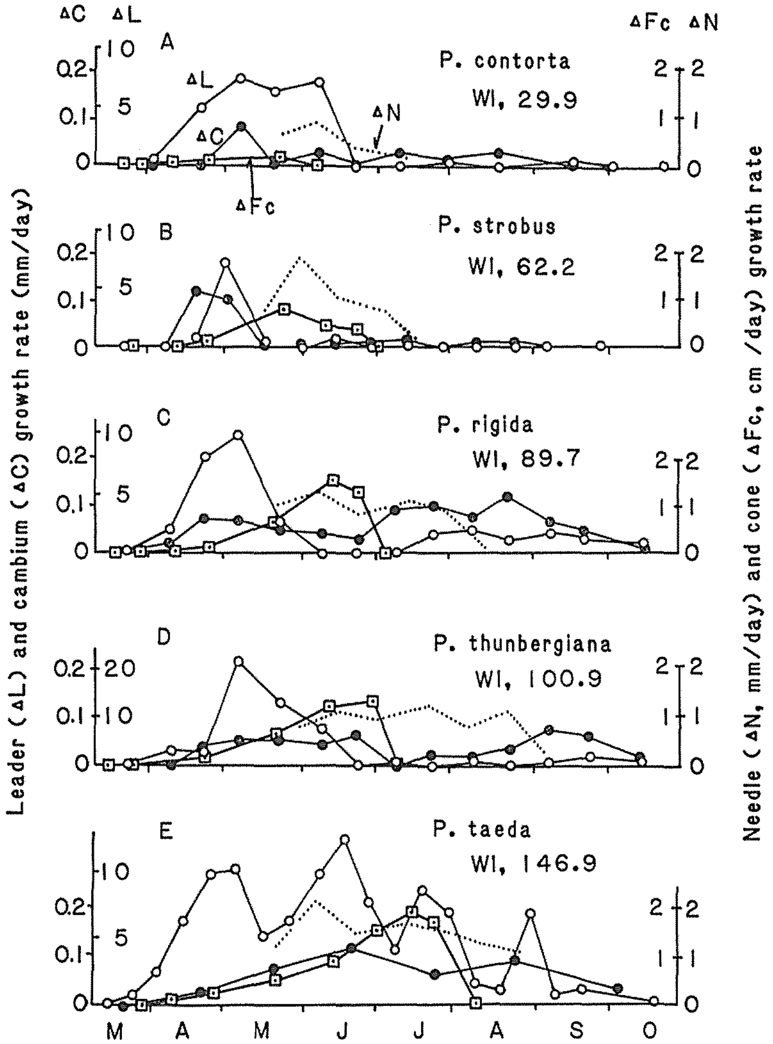

Fig. 7. Five samples of seasonal growth course of 2nd-year cones with growth rates of leader, needles and cambium. Completion of cone growth is delayed by thermal conditions, i. e., by Warmth Index (WI) in native regions in each species.

seasonality adaptation of each species to the climatic conditions of the original distribution. The demonstrated interrelations are typical examples mainly basing on a classification according to shoot growth types. As the genus *Pinus* has numerous species which are distributed world wide, many variations in the interrelation between growth seasonality of various plant parts are to be expected.

Even in the genus *Pinus*, the Contorta and Taeda types are restricted to few subsections. All species of the subgenus *Strobus*, which is classified into 2 sections, 5 subsections and 31 species, are of uninodal type. Among the 2 sections, 8 subsections and 61 species of the subgenus *Pinus*, typical representatives of the Taeda type are only ca. 10 species.

Most of them belong to the two subsections of *Australes* and *Oocarpae.* The Cortorta type is represented by some species of the subsection *Sabiniane,* the subsection *Oocarpae* and subsection *Contortae.*

Except for *Pinus halepensis* and *Pinus insularis,* both Contorta and Taeda types are distributed only in North America and Central America, whereas in Eurasia only uninodal pines (OOHATA[6]). *Pinus halepensis* and *Pinus insularis* are Taeda type pines in subsection *Sylvestres,* and distribute respectively at Mediterranean region and South East Asia. Although there are two species of subsections in *Sylvestres* in North and Central America, both species are uninodal type (SHAW[1]) . When the terminal buds are able to continue growth the same season, the Taeda type pine will be specialized to long growing season. Although the form of new shoot of Contorta type is different from both the uninodal and the Taeda type, the Contorta type and Taeda type may be intimately related. Both types are sometimes classified together in the same subsection, e. g. pines of subsection *Contortae* can be separated into three species of Contorta type and one species of Taeda type. In this group, the main type may be the Contorta type. In contrast, in the subsection *Australes* more species blong to the Taeda type than to the Contorta type. It should be mentioned that all three types are represented in the subsection *Oocarpae.*

As mentioned before, the pattern of pine shoot growth is complicated one. In order to understand the diversity of the nature in pines, furthermore analysis is need relating to the life pattern or seasonality of respective pine species.

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